

BIOLOGY AND EVOLUTION OF THE *ATLAPETES SCHISTACEUS* SPECIES-GROUP (AVES: EMBERIZINAE)

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ABSTRACT

Atlapetes schistaceus, *nationi*, *leucopterus*, *albiceps*, *pallidiceps*, and *rufigenis*, ranging in the subtropical and temperate zones of the high Andes from Colombia to Peru, form a species-group. The six species are thought to have originated in the Pleistocene. The present distribution of *A. schistaceus* closely approximates the presumed location of lowland forest refugia during warm-dry interglacial periods. The remaining five species appear to have had their origins in small moist pockets, also during warm-dry interglacial periods, within the high Andes of Ecuador and Peru, either as derivatives of ancestral *schistaceus* or of more recently arisen species within the species-group.

INTRODUCTION

Atlapetes, a genus of secretive brush-inhabiting emberizines, occurs at high elevations from the northern Mexican plateau southward through Middle America to northern South America, east to southeastern Venezuela and immediately adjacent Brazil, and south through the Andes to southern Peru, Bolivia, and northwestern Argentina. Twenty-two species of *Atlapetes* are currently recognized (Paynter, 1970: 190-206), seventeen of these occur in the northern Andes between northern Colombia and southern Ecuador.

Within the genus there are six species, viz., *schistaceus*, *nationi*, *leucopterus*, *albiceps*, *pallidiceps*, and *rufigenis*, which are morphologically similar and which appear to be more closely related to one another than to other members of the genus. The

six species might be considered as comprising a superspecies, but until more is known of the apparent partial sympatry of several forms it seems better to treat them simply as the "*A. schistaceus* species-group." The group is distributed from northern Colombia and western Venezuela south to southern Peru, with particularly complex and interesting distributional patterns in southern Ecuador and northern Peru (Fig. 1). However, as is true of most species of *Atlapetes*, the ranges of these birds are known only in broad outlines and there are very few published accounts of any aspects of their biology.

Because a meaningful analysis of the origin and evolution of such an assemblage is difficult without knowledge of the living birds, it was decided to study the species-group in Ecuador, where, of the six species, only *rufigenis* fails to occur. In June 1965 David W. Norton went to Loja, the southernmost province of Ecuador, in order to reconnoiter localities where the various species could be studied. Norton found *leucopterus* at Cruzpamba on the Río Celica and *albiceps* at Yamana in the upper Casanga Valley, as well as other species of the genus not relevant to the present paper. My field work began in October. We had planned to spend the three months of the first field season working northward from the southern border of the country, becoming familiar with the species and mapping their distribution.

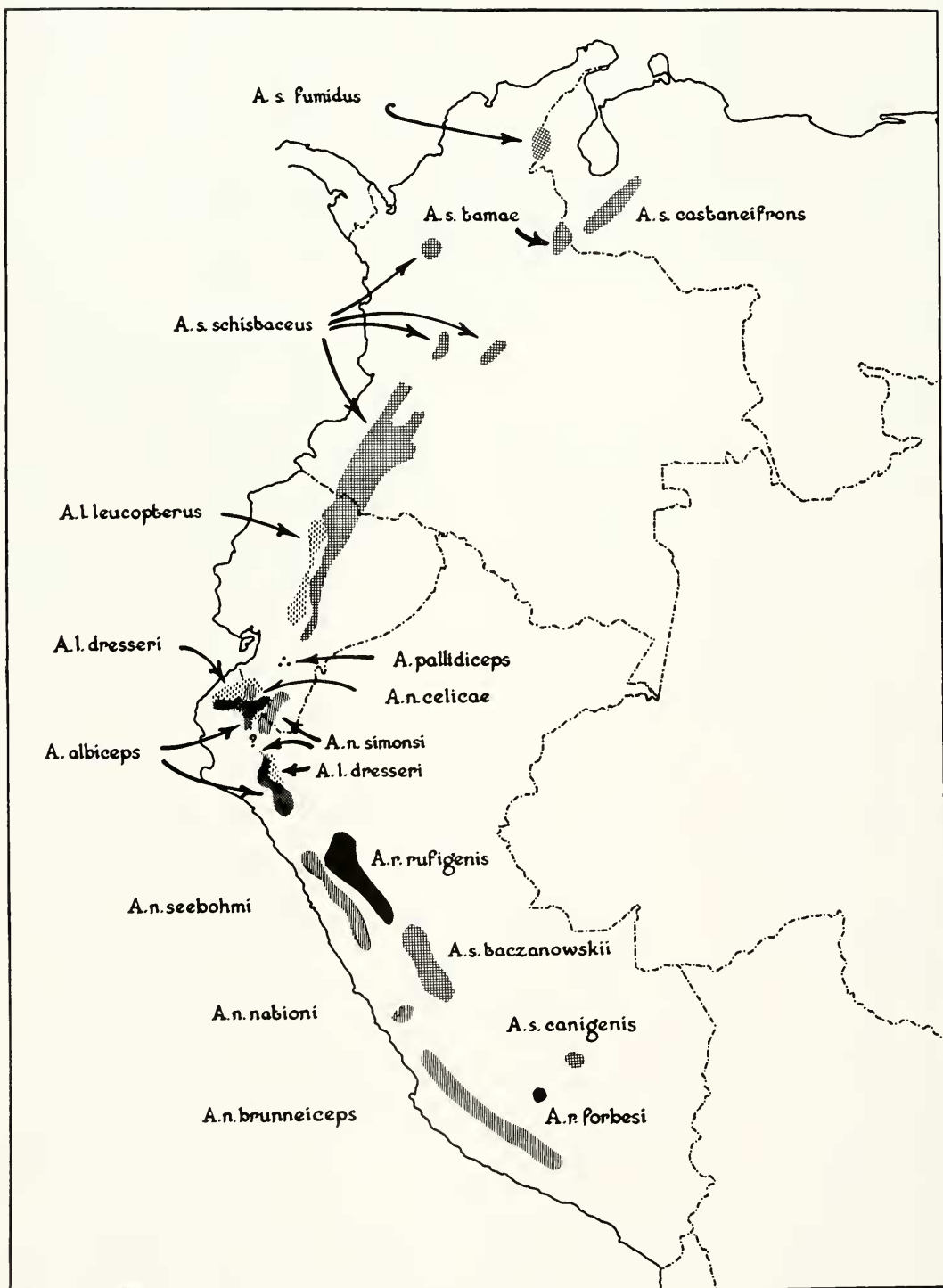


FIGURE 1. Distribution of the *Atlapetes schistaceus* species-group.

More detailed studies of their biology and distribution were scheduled for future seasons. By early November we had reached Las Palmas, a settlement in the valley of the Río Paute, east of Cuenca, Azuay. Here our party was attacked by a band of villagers, resulting in almost fatal injuries and causing abandonment of plans for further field work.

I was fortunate in having been able to observe four of the six species of the group, viz., *nationi*, *leucopterus*, *albiceps*, and *pallidiceps*. Although these observations were hardly more than an introduction to the living birds, they do provide a better insight into the complexities of the species-group than was available heretofore.

ACKNOWLEDGMENTS

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DISTRIBUTION, HABITS, AND MORPHOLOGY

Atlapetes schistaceus

Range. *A. schistaceus* has the most extensive range of the six forms within the species-group (Fig. 1). It occurs in the northernmost extensions of the Andes in the Sierra de Perijá of northeastern Colombia and northwestern Venezuela and as far east as the Cordillera de Mérida of western Venezuela.

One race, *fumidus*, is known only from the northern portion of the Sierra de Perijá. It may be isolated there because of the generally lower elevation of the southern part of the cordillera. However, the race is the least distinctive of the six recognized and I suspect that gene flow between *fumidus* and nearby races is facilitated by the presence of yet undiscovered semi-isolated populations in the small areas with altitudes in excess of 2,000 m that form an irregular chain through the southern half of the Sierra de Perijá. Another race, *castaneifrons*, occurs in Venezuela from eastern Táchira northeast to Trujillo and apparently is separated from *tamae*, the form of western Táchira and adjacent Santander, Colombia, by the arid valley of the Río Torbes, a known barrier to other birds (Vuilleumier, 1971).

Although the records are sparse and spotty, the species seems to be found at higher elevations on both the eastern and western slopes of all three Andean ranges in Colombia (de Schauensee, 1951; Phelps and Phelps, Jr., 1963). There are, however, large segments in each cordillera from which the species has not been recorded. Presumably the mountains are too low here for the species to occur, with the result that there are probably several isolated populations as, for example, on Nudo Paramillo in Antioquia.

In Ecuador the species is known from numerous records on the eastern slope south to Tungurahua, but south of here there exist only two records, one from the

TABLE 1. COMPARATIVE MEASUREMENTS OF *A. SCHISTACEUS* SUBSPECIES.

Race	Sex	Wing (flat)				Tail				Culmen (fr. base)			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
<i>fumidus</i> ¹	♂	14	71.2-77.7	74.5 mm		14	73.2-82.8	78.6 mm		14	14.2-15.2	14.8 mm	
<i>castaneifrons</i> ²	♂	3	73-77	75.0	2.0	3	76-81	78.3	2.5	2	16	16.0	
<i>tamae</i> ³	♂	?	74-78			?	79-82						
<i>schistaceus</i> ²	♂	3	73-84	78.6	5.4	4	73-87	80.0	6.6	4	14-15	14.3	0.5
<i>taczanowskii</i> ²	♂	4	78-81	79.0	1.4	4	82-84	83.5	1.0	4	15-17	15.6	1.0
<i>canigenis</i> ⁴	♂	1	76			1	78			1	15.5		
<i>fumidus</i> ¹	♀	16	66.4-72.9	69.9		16	69.7-78.0	78.0		15	14.3-15.8	14.8	
<i>castaneifrons</i> ²	♀	5	68-74	70.4	2.3	5	69-77	72.8	3.5	5	14-17	15.8	1.3
<i>tamae</i> ³	♀	?	73-74			?	76-78						
<i>schistaceus</i> ²	♀	7	77-83	79.4	2.0	7	78-85	80.8	1.5	7	14-16	15.4	0.5
<i>taczanowskii</i> ²	♀	3	71-77	74.3	2.9	3	75-81	77.3	3.2	3	16-17	16.3	0.6
<i>canigenis</i> ⁴	♀	1	72			1	72			1	15		

¹ Wetmore and Phelps, Jr., 1953: 13-14.² Original data.³ Hellmayr, 1938: 404.⁴ Chapman, 1919: 330.

upper Río Upano (Chapman, 1926), which apparently is in Zamora near the border of Chimborazo, and one from Las Palmas, northeastern Azuay (specimen in Moore Collection, Occidental College). On the western slope the species barely enters Ecuador. One specimen has been taken on "the road to Nanegal," northern Pichincha (Chapman, 1926) and one from a short distance farther north at Intag [= Intac], southwestern Imbabura (Berlepsch, 1912).

An 800-km break in the distribution occurs between southern Ecuador and northern Peru with the species (race *taczanowskii*) reappearing in Huánuco and Junín, again on the eastern slope of the Andes. Its southern limit appears to be the Urubamba Valley, central Cuzco (race *canigenis*). It has not been recorded between Junín and Cuzco. This wide gap is probably an artifact attributable to the absence of observers, although a smaller discontinuity almost certainly exists owing to the presence of the arid valley of the Río Apurímac.

A. schistaceus is a high altitude form, ranging from 1,850 m to as high as 3,750 m, with the majority of records from about

2,500 to 3,000 m. There are insufficient data to detect any geographic variation in altitudinal range.

Habitat. Most authors (e. g., Chapman, 1917, 1919, 1921, 1926; and de Schauensee, 1951, 1964) describe the species as occurring in the subtropical and humid temperate zones. The only specific indications of its habitat seem to be those of Wetmore and Phelps, Jr. (1953), who mention the northernmost race (*fumidus*) as occurring in woodlands, and Zimmer (1930), who describes a Peruvian race as being found on the ground under bushes and in other shady places.

Habits. Except for a brief comment by Zimmer (1930) that the species scratches on the ground in the manner of towhees (*Pipilo*), there is no information about the living bird.

Morphological variation. In spite of the species' extended range and the existence of several major discontinuities, there appear to be no significant differences between the various named populations in wing, tail, or bill lengths (Table 1). The data suggest that the races *schistaceus* and *taczanowskii* might be larger than northern

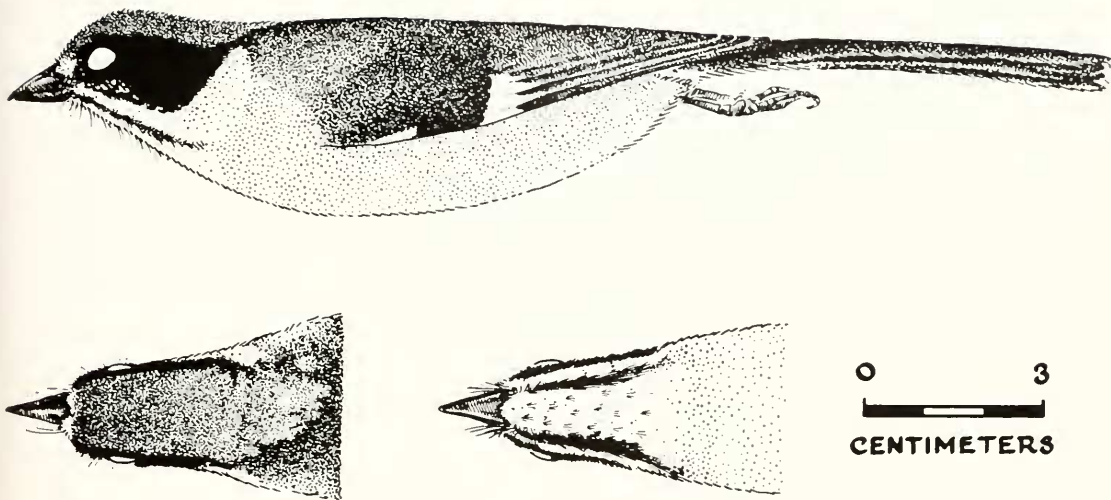


FIGURE 2. *Atlapetes s. schistaceus*. Oyacachi (2,500 m), Pichincha, Ecuador. ♀. MCZ 139,387.

Andean populations, but there are too few measurements to be certain. The species does, however, exhibit moderate sexual dimorphism in size. On the other hand, there is no sexual dimorphism in color and pattern but there is considerable geographic variation in these characters; these differences have been used in describing the six recognized races.

Nominate *schistaceus* (Fig. 2), which ranges through the Colombian Andes, except in the northeast, is characterized by a sooty, nearly black, back and black tail. The pileum is dark chestnut with a narrow area of black over the bill. The lore is extensively white and the side of the head is black with slightly lighter auriculars and a broad grayish white malar streak extending to the neck. The mystacial streak is broad and long. The throat is grayish white with an admixture of black feathers; the breast, abdomen, and sides are dark gray, lightening somewhat toward the mid-line. At times the portion of the upper breast adjacent to the throat patch is somewhat scalloped by black tips to the feathers. A conspicuous white alar speculum, varying moderately in size, characterizes the black wing. The concealed

bend of the wing is white and occasionally there is a restricted area of white on the exposed base of the outer edge of the outermost primary.

A. s. tamae, which is not contiguous with nominate *schistaceus* or with *castaneifrons*, has a black back as well as tail. The crown and neck are a lighter chestnut than in the nominate form and there is only a faint trace of black above the bill. The sides of the head are black with no lightening in the auricular region; the lores are black or indistinctly dark gray. The malar streak is short and narrow, as is the mystacial streak. The throat is grayish white and sharply demarcated from the dark gray underparts, although there is still a tendency toward a lighter color on the abdomen. The wing is black with no speculum, but the concealed bend of the wing remains white.

A. s. castaneifrons, the form of western Venezuela, is similar to *tamae* except for lighter pileum and hindneck, a small white loreal spot, and no trace of black over the bill. The malar streak is broader and whiter and the mystacial streak heavier. There is a tendency for the outer web of the outermost primary to be pale, reminis-

cent of the condition in the nominate form, and a faint suggestion of an alar speculum is evident in some specimens.

The race *fumidus*, from the northern Sierra de Perijá, is the least distinctive of the six subspecies. It is very similar to *castaneifrons* and differs from it in being less black dorsally and more uniformly gray on the breast and abdomen.

A. s. taczanowskii, the race isolated on the eastern slopes of central eastern Peru (Fig. 1), resembles *castaneifrons* except that its back is more sooty, there is no hint of a speculum or a white edge to the edge of the wing, and the lores are nearly white with the white extending to the sides of the forehead, accenting a pronounced area of black at the base of the bill.

The southernmost race, *canigenis* of the Cuzco region, differs from all other forms in lacking both the malar and mystacial streaks. Otherwise it is similar to *taczanowskii*, except that the lores are dark gray and the black at the base of the bill is replaced by dark gray, thus forming a gray band from eye to eye.

In summary, the main differences between the races are as follow. The pileum is darkest in nominate *schistaceus*, lighter in *tamae*, and is lightest, and similar, in *castaneifrons*, *fumidus*, *taczanowskii*, and *canigenis*. The alar speculum occurs only in nominate *schistaceus* but is faintly suggested in *castaneifrons*. White edging at the base of the outermost primary is found in some examples of *A. s. schistaceus*, and there is a tendency toward paleness on the web in some examples of *castaneifrons*, but in the remaining races the primaries are completely dark. Mystacial and malar streaks are found in various widths and lengths in five races but are entirely lacking in *canigenis*. Lorai spots are pronounced in nominate *schistaceus*, very large in *taczanowskii*, small in *castaneifrons* and *fumidus*, nearly absent in *tamae*, and dark gray and concolor with the forehead in *canigenis*. The forehead is conspicuously black in *schistaceus*, very

narrowly black in *tamae*, black with white edges in *taczanowskii*, gray in *canigenis*, and concolor with the crown in *castaneifrons* and *fumidus*.

Atlapetes nationi

Range. This species has an extensive range from southern Ecuador to southern Peru (Fig. 1). It is known from three localities in Loja, Ecuador, all of which are on the western slope of the Andes, although the type locality, which is the town of Loja, is nearly astride the continental divide. Presumably the Loja specimens were taken on the range to the west of the town, where Norton (personal communication) saw two birds at about 2,400 m in October 1965.

The next known occurrence of the species is some 200 km to the south in the Porculla Valley, east of Olmos, Lambayeque, Peru. The two specimens from here (Markl Collection, Basel Museum) are referable to *A. n. simonsi*, the race also occurring in Loja. The species reappears in Libertad and seems to have an interrupted range along the western slope south to Arequipa, southwestern Peru. There are two large distributional gaps on either side of the nominate race. The southern gap is probably an artifact, owing to the absence of collectors. The northern gap may be real; the marked difference between the races on either side suggests a broken distribution.

The type of the nominate form, which is lost, is said (Hellmayr, 1938) to have come from Ninarupa, Junín, which would place the species on the eastern slope. This is doubtless an error, as concluded by Koepecke (1958) and de Schauensee (1966).

A. nationi has been found at altitudes from 1,870 to 3,500 m.

Habitat. In contrast to *A. schistaceus*, the habitat requirements of *A. nationi* are well known, mainly through the work of Koepecke (1958; 1961; 1964), who describes it as inhabiting temperate brush and forests.

I observed the species in early October 5 km southeast of Gonzanamá at an altitude of 2,300 m. The area is subtropical, dry but not arid (small fields of sugar cane are grown without irrigation on the less steep slopes), with many fields and pastures. Areas unsuited for agriculture are heavily cut for firewood. The ridges, which have only a thin layer of soil and are drier than farther downslope, are covered with a low dense scrub about chest-high. *A. nationi simonsi* was found here. *A. torquatus*, a humid region form, was also noted in the area, but only in an isolated patch of woods about 7 m in height with a dark understory.

The locality where Norton observed *A. nationi* on 24 October is situated on the mountain between Loja and Catamayo. This is a vast region of apparently naturally occurring scrub similar to the small area where we found the species near Gonzanamá.

We did not find *A. n. simonsi* in woodland, in contrast to Koepeke's observations in Peru of *A. n. nationi*, *brunneiceps*, and *seebohmi*. It would seem that where *A. nationi* occurs in the temperate zone, as in most of Peru, it is a forest species but where it descends to the semi-arid subtropical zone, as does *A. n. simonsi*, it occurs in scrub, possibly because of the presence of *A. torquatus* in the wetter and taller woods. This will be considered more fully in a subsequent study of *A. torquatus*.

Habits. Eight specimens were collected near Gonzanamá over a period of several days. All were taken from small flocks; four specimens are known with certainty to have come from flocks consisting of but three birds. They were very secretive, generally keeping low in the dense brush but frequently uttering a loud metallic "seep seep." It is of interest that, in contrast to my experience, Koepeke (1958) describes the call in Peru as consisting of a single soft "zieh," although she does note that in the breeding season the song is strong and loud.

When birds were flushed and forced to fly from one clump of brush to another, their wings made a noticeable noise. Koepeke (1964) mentions the bird's habit of raising its tail but, although we often heard individuals scratching among dry leaves, we never glimpsed them on the ground.

There were no indications of breeding; presumably the breeding season is during the rains, as has been noted in Peru (Koepeke, 1958).

Food. Two stomachs were preserved. One contained a large dipterid, the body of an unidentifiable large insect, a few small seeds, and some grit. The other had finely ground bits of chitin, fragments of seeds, and a considerable quantity of grit. Most of the latter was bright reddish brown; a few particles were clear quartz.

Peruvian specimens examined by Koepeke (1958) had fed on few insects but had eaten fruit and plant material, none of which occurred in the Gonzanamá material. I imagine that these differences in food are related to the season in which the specimens were collected, rather than to any fundamental differences in diet.

Morphological variation. Although the data are scanty, there appears to be a general increase in size, particularly in weight, from north to south (Table 2). On the other hand, regional differences in color and pattern are pronounced.

A. n. simonsi (Fig. 3), which is known from the type and one other specimen collected at (= near?) Loja (Chapman, 1921), from eight specimens taken by us near Gonzanamá and from two specimens from the Porculla Valley, Lambayeque (Markl Collection, Basel Museum), is dark sooty gray on the back and wings, with a nearly black tail. It is lighter than any race of *A. schistaceus*, but not markedly different. The pileum is light chestnut, very closely resembling the head color in *A. s. castaneifrons*. The feathers over the nares are black. There is a dirty white supraloral spot and the side of

TABLE 2. COMPARATIVE MEASUREMENTS OF *A. NATIONI* SUBSPECIES.

Race	Sex	Wing (flat)				Tail				Culmen (fr. base)				Weight			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
<i>simonsi</i> ¹	♂	3	75-79	77.3 mm	2.1	3	75-81	77.3 mm	3.2	3	15-16	15.6 mm	.6	3	31.2-33.1	32.1	.9
<i>celicae</i> ²	♂	1	68.5			1	63 (worn)			1	16						
<i>seebohmi</i> ³	♂	?	74-81			?	80-87			?	15-16						
<i>nationi</i> ¹	♂	1	82			1	80			1	19			2 ⁴	41.5-43.4	42.5	
<i>simonsi</i> ¹	♀	2	71-75	73.0		1	73			2	15-16	15.5		4	27.1-37.1	31.4	4.2
<i>seebohmi</i> ³	♀	?	74-76			?	75-77			?	14-15						
<i>nationi</i> ¹	♀	1	83			1	76			1	19			2 ⁴	40.5-41.0	40.8	
<i>brunneiceps</i> ⁵	?	?	81-87			?	78-87			?	15-16.5			3 ⁶	38.3-43.1	40.2	.3

¹ Original data.² Chapman, 1925: 7.³ Hellmayr, 1938: 402.⁴ Koepcke, 1958: 179.⁵ Hellmayr, 1938: 412; measurements not divided by sex.⁶ Koepcke, 1958: 180; 2 ♀, 1 ♂.

the head is black, lightening slightly in the auricular region. Below, the bird is white from throat to abdomen, with a band of gray across the breast which pales considerably in the center. There is a wash of buffy on the lower abdomen which intensifies on the crissum. The flanks and sides are dark gray. The very light colored venter is the most distinctive character distinguishing *simonsi* from all races of *A. schistaceus*. There are broad black mystacial stripes and a black line at the base of the mandible. The malar stripe is white, merging into the white of the throat. The outer web of the ninth primary is white and the outer half of the outer web of the eighth primary is gray.

A. n. celicae, which is known only from the type that is said to have been taken at Celica, only about 65 km west of Gonzanamá, offers a problem. It very closely resembles *simonsi* except that its wing is much smaller (Table 2) and it has a narrow dark area above the nares, a character tending toward the very dark forehead in *seebohmi*. It is slightly buffy on the chin, a feature not noted in any specimens of *simonsi* but which is a tendency toward the condition in nominate *nationi*. Chapman (1925; 1926), in contrasting this form with *simonsi*, remarked that the supraloral spot is obsolete, but I find it as prominent as in my series of *simonsi*.

In 1965 we searched extensively for this race in the vicinity of Celica (see Paynter, 1970: 197) but failed to find it. The type was said to have been collected at an altitude of 6,900 ft. However, Celica is considerably lower than this and it is probable that the bird was taken northeast of the town toward Mt. Guachanamá. We collected for several days near the village of Guachanamá (alt. 2,500 m), finding *A. rufinuucha* common. Presumably this locality is too moist for *A. nationi*.

For the present, therefore, we must accept the race *celicae* although eventually it may be found to be an aberrant example of *simonsi*.

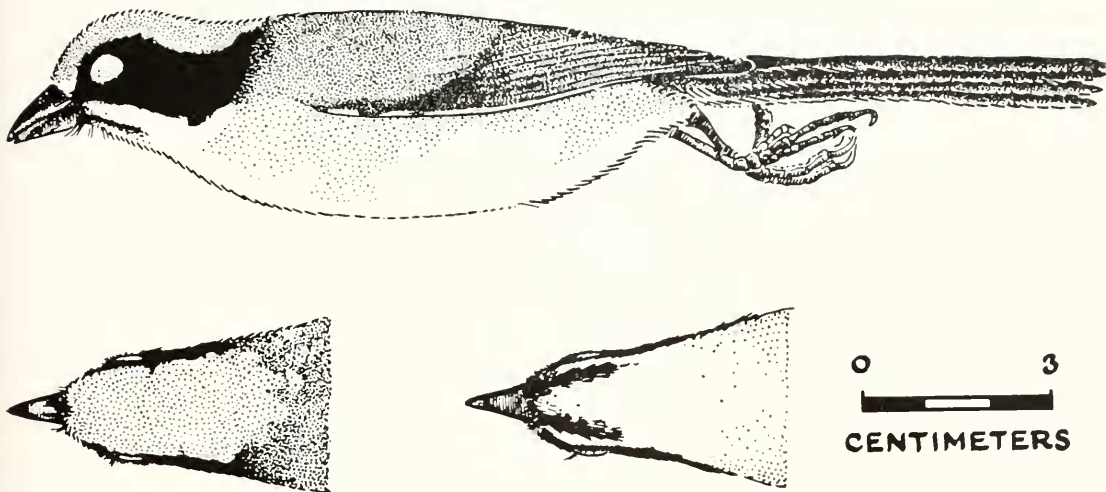


FIGURE 3. *Atlapetes nationi simonsi*. 5 km southeast Gonzanamá (2,300 m), Loja, Ecuador. ♂. MCZ 288,145.

A. n. seebohmi (Fig. 4), which ranges from Libertad to Ancash (Fig. 1) and which doubtless will be found to merge in the north with *simonsi*, but probably not in the south with nominate *nationi*, is closely similar to *simonsi*. Its back, wings, and tail are distinctly more olive gray, the breast band is broader and with only a slightly lighter area in the center, the crown is darker chestnut, and there is a broad band of black on the forehead. The gray edge to

the eighth primary that is found in *simonsi* seems to be lacking in this form, but this feature is only evident in very fresh plumage in *simonsi* and I have seen no comparable specimens of *seebohmi*.

A. n. nationi (Fig. 5), which is known to occur only in a limited area to the east of Lima, differs fairly substantially from the preceding two forms in that instead of the pileum being chestnut it is reddish black, blending into the black of the sides of head

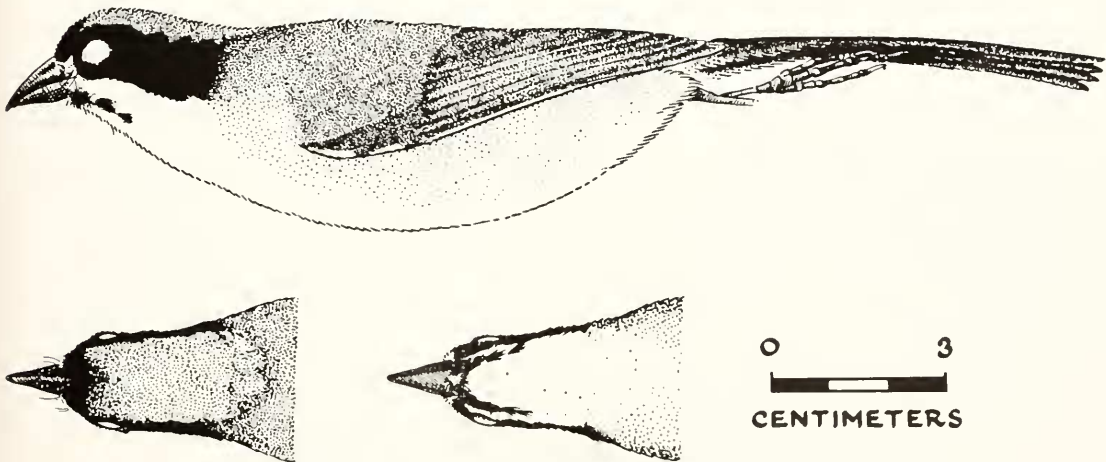


FIGURE 4. *Atlapetes nationi seebohmi*. Macate (alt. ?), Ancash, Peru. ♂. MCZ 287,193.

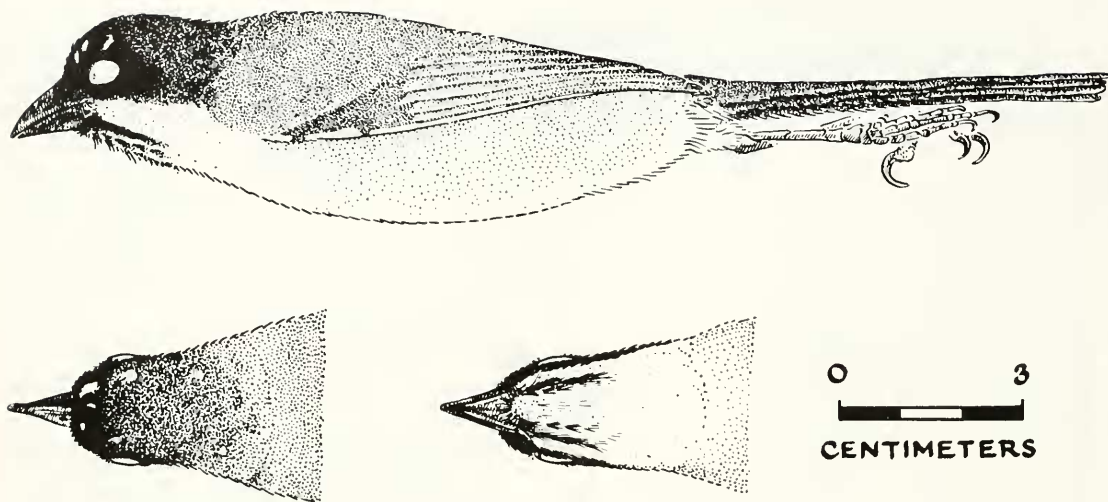


FIGURE 5. *Atlapetes n. nationi*. Canta (2,400 m), Obrajilla, Lima, Peru. ♂. MCZ 179,157.

and forehead. Scattered white feathers on the head appear quite frequently. The back is suffused with brown. The breast band is similar to that in *seebohmi* but the abdomen is dark buffy, paling in the center and where it meets the breast band, and darkening dorsally. The crissum is dark buff. The areas between the mystacial streaks and on both sides of them are washed with buff. The mystacial streaks are short but broad and without sharp borders, merging into a pronounced area of black at the base of the bill. The ninth primary again has a white outer web and the next two or three remiges have dark grayish outer borders.

The last race, *A. n. brunneiceps*, which has an extensive range from southern Lima province to Arequipa, resembles the nominate form except that it is lighter gray dorsally and the pileum and sides of the head are more brown, less reddish. The chin and malar region are more distinctly buffy. Scattered white feathers appear on the head as in *A. n. nationi*.

In summary, the three northern races are closely similar, differing mainly in the presence or absence of black on the forehead and in the depth of color of the breast

band and pileum. The two southern races are heavier, and probably larger, than those of the north, have no chestnut on the pileum, and are distinctly rufous ventrally. They differ between themselves chiefly in dorsal coloration.

Atlapetes leucopterus

Range. *A. leucopterus* has a more restricted distribution than the previous two species, occurring on the western slopes of the Andes from northern Ecuador south to extreme northern Peru (Fig. 1). The northernmost recorded occurrence is "on the road to Nanegal," a classic source of material for local collectors near Quito. *A. schistaceus* has also been taken at this generalized locality, but whether the two species are sympatric or separated altitudinally is unknown.

There are a number of records from the vicinity of Quito, but the next known occurrence is 150 km south at Sinche, which is northeast of Guaranda in the province of Bolívar. The absence of records from intermediate points is almost certainly because the slopes in this region are not readily accessible to collectors. The species has been noted at several localities in the

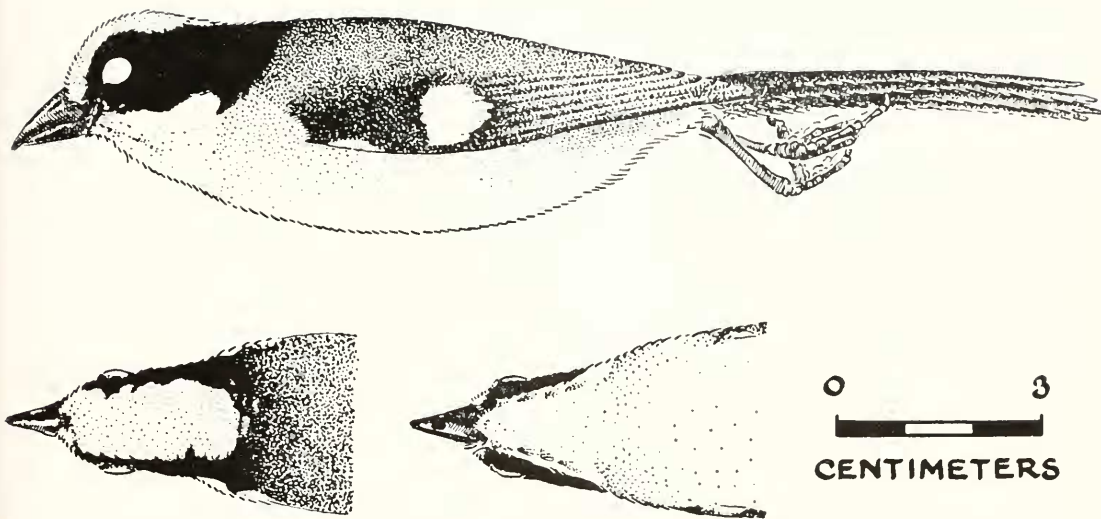


FIGURE 6. *Atlapetes l. leucopterus*. Valle Tumbaco (2,300 m), Pichincha, Ecuador. ♂. MCZ 288,135.

nearby Chimbo Valley in southwestern Chimborazo province, an area long accessible by train, but then there is another wide breach in the distribution, this time in excess of 200 km, with the species re-appearing in southwestern Loja and in Piura and Lambayeque of adjacent northern Peru. Although the slopes are perhaps even more difficult to reach in southwestern Ecuador than farther north, there is a possibility that the southern distributional gap may be real and not the result of the vagaries of collectors. This seems probable because the birds from the southern limits of the range are morphologically very distinct from those on the other side of the presumed gap, i.e., those from central Ecuador, while those birds from northern Ecuador are indistinguishable from those of central Ecuador. The distance between the central and northern population samples is roughly the same as that between the central and southern samples, which suggests that the morphological distinctness of the southern population is the result of restricted gene flow.

In addition to the possible sympatry of this species with *A. schistaceus* north of Quito (see above) there are two other

areas of interest. *A. l. dresseri* is known to be sympatric with *A. nationi simonsi* in the Porculla Valley, Lambayeque. Specimens in the Markl Collection (Basel Mus.) from the latter locality bear the annotation that the two species occur in the same flock. *A. l. dresseri* is also known to be sympatric, or at least parapatric, with *A. albiceps* in Piura in the somewhat isolated Cerros de la Brea in the vicinity of Sullana (specimens in Markl Collection and in Mus. Zool., Louisiana State Univ.).

The nominate form has an altitudinal range of from about 600 to 2,900 m, while *A. l. dresseri*, the southern race, has been found from 700 to 2,550 m.

Habitat. There seems to be no published description of the habitat. At Alamor, Loja, the only place where I have seen the species, it was found in viney thickets in an area of moderately moist subtropical vegetation.

Distributional records seem to indicate that while the species is found in the humid subtropics it may be most common in the arid subtropical zone. It also ranges into the arid temperate zone, at least in the vicinity of Quito.

TABLE 3. COMPARATIVE MEASUREMENTS OF *A. LEUCOPTERUS* SUBSPECIES.

Race	Sex	Wing (flat)			Tail			Culmen (fr. base)			Weight		
		N	Range	Mean	N	Range	Mean	N	Range	Mean	N	Range	Mean
				SD									
leucopterus	♂	2	70-71	70.5	2	65-67	66.0	1	17				
dresseri	♂	1	68					2	14	14.0	2	20.7-22.7	21.4
leucopterus	♀	3	67-69	68.0	3	62-65	63.0	3	16-17	16.7			
dresseri	♀	1	65	.71	1	63		2	14	14.0	1	26.1	
										.47			

Habits. Again there seems to be no published description of the habits of this species. I observed a flock of three, or possibly more, birds for a brief time at Alamor. The birds were feeding in vines about two feet from the ground. Their white alar patches were very conspicuous and seemed to accent their quick movements as they searched the vegetation. This activity contrasted sharply with the slower, more deliberate, motions of a flock of *A. torquatus*, which was on the ground below, turning leaves with their bills and riffling the litter.

Food. One stomach, from a specimen collected at Alamor, was examined. Its food consisted entirely of ants. Interestingly, the grit it had consumed was mainly dark colored and rounded, in distinction to the bright and sharp fragments noted in *A. schistaceus* and *A. nationi*.

Morphological variation. *A. leucopterus* (Fig. 6) is essentially a small replica of *A. schistaceus* (in particular the nominate form, which has an alar patch) or of one of the brown-capped northern races of *A. nationi*.

The species has been divided into two races on the basis of color and pattern. I have seen little fresh-plumaged material of either race, but from limited measurements (Table 3) it appears that nominate *leucopterus*, the more northern form, may be larger. The length of the bill is almost certainly greater; the bill is proportionately more massive.

A. l. dresseri is also distinguished by an overall buffy tone. The white throat, chest, and abdomen are replaced by buffy white, the gray flanks are markedly buffy, and even the gray of the back has a foxy tone. In addition, the buffy white supraloral spots are larger in *dresseri* than in the nominate race and sometimes are so extensive they meet, forming a white forehead. In *A. l. leucopterus* a restricted area between the supraloral spots may be black or there are black feathers mixed with the chestnut, which extends forward from the

TABLE 4. COMPARATIVE MEASUREMENTS OF *A. RUFIGENIS* SUBSPECIES.

Race	Sex	Wing				Tail				Culmen (fr. base)			
		N	Range	Mean	SD	N	Range	Mean	SD	N	Range	Mean	SD
<i>rufigenis</i>	♂	6	86-98	90.5	3.98	5	89-98	91.6	3.65	6	18	18	
<i>forbesi</i> ¹	♂	4	77-81	80.5	2.89					4	16-17	16.25	.06
<i>rufigenis</i>	♀	1	92			1	95			1	19		
<i>forbesi</i> ¹	♀	1	74										

¹ Morrison, 1947.

crown. In *A. l. dresseri* there is always an extensive area of black on the fore-crown, a character not present in *A. l. leucopterus*. However, it is the variation in the extent of the black area that is particularly noteworthy. It ranges from a small area equal in size to the white postnasal band to complete coverage of the front half of the head. In the specimen taken at Alamor the black stripes which laterally border the chestnut crown in both races are so extensive that the chestnut is reduced to a triangular area with its slim apex in the center of the crown and its narrow base at the nape. All the specimens of *dresseri* that I have seen have white eye rings, whereas this character is lacking in nominate *leucopterus*. However, as in the variation in the amount of black on the head, the size of the eye ring varies enormously. It may be a narrow ring which contrasts with the black superciliary stripe and the near-black auriculars and circumocular region, or it may range up to a wide irregularly shaped ring that meets the supraloral spot, obliterating the black lores, and encroaching on the crown's lateral stripes, thus creating a bird whose cheeks are mainly white rather than black.

Mystacial streaks are characteristic of both races. They are indistinct in the nominate form but more pronounced in *dresseri*, although in the latter they vary in size and intensity.

In summary, *dresseri* is distinguished from nominate *leucopterus* by its smaller bill (and possibly wing and tail), more buffy coloration, black forehead, the presence of a white eye ring, and more pro-

nounced mystacial stripes. *A. l. dresseri* exhibits unusually great variation in some of the characters that distinguish it from the nominate subspecies.

Atlapetes rufigenis

Range. *Atlapetes rufigenis* has a markedly restricted range. The species occurs in the highlands of northern Peru within the drainage system of the upper Río Marañón from Libertad and extreme southern Cajamarca south to Huánuco. There is then a breach in the distribution of about 650 km and the species reappears in Apurímac, where it is known from one locality in the valley of the Río Pampas, which is a tributary of the Río Apurímac.

Altitudinally the northern population has been found between 2,800 and 4,000 m but most records are from about 3,250 m. The southern population is known to occur at approximately 2,750 m.

Habitat. Zimmer (1930) reported collecting a single specimen of nominate *rufigenis* at Cullcui, Huánuco, from a jumble of vines and bushes that formed a semi-humid oasis in an otherwise arid subtropical region. Morrison (1948) collected ten specimens of the southern form (*A. r. forbesi*) at Pomayaco in dense tangles in the humid temperate zone.

Habits. Morrison (1948) reported *A. r. forbesi* to be silent and very secretive. I have seen one specimen from Yámac, Ancash, which is said to have had moderately enlarged testes on 21 March.

Morphological variation. *A. rufigenis* is the largest member of the species group (Table 4). In color and pattern it is much

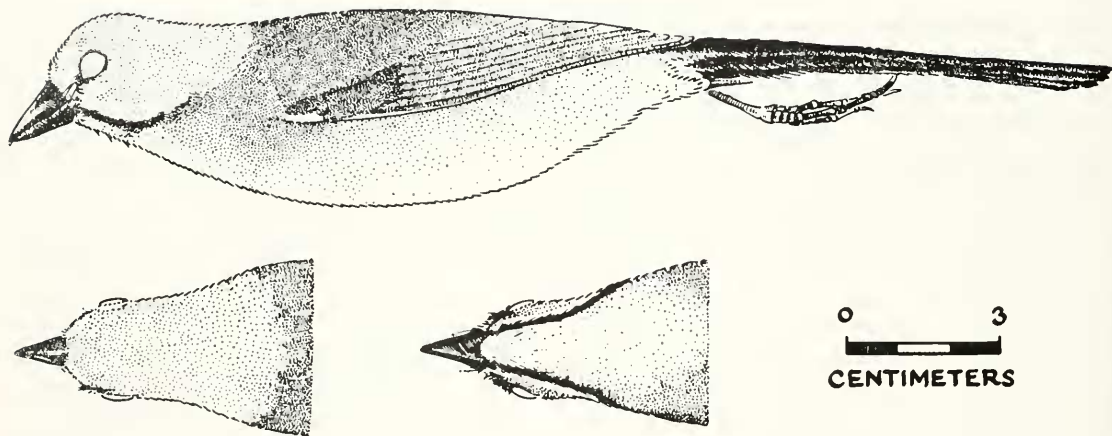


FIGURE 7. *Atlapetes r. rufigenis*. Yáñac (3,700 m), Ancash, Peru. ♂. MCZ 179,163.

like *A. nationi seebohmi* or *A. n. simonsi*, except that the black on the sides of the head is either absent or reduced and replaced by the chestnut of the crown (Fig. 7).

In nominate *rufigenis* the lores are either white or gray and the supraloral region is buffy white. In some instances the pale supraloral areas almost meet above the bill. The sides of the head are concolor with the crown, except that in one of seven specimens examined there is an indistinct black eye ring and a few small black feathers in the auricular region. The outer edge of the outermost primary is a pale dirty gray which, while evident, does not sharply contrast with the rest of the wing, as it does, for example, in *A. n. simonsi*. The chestnut of the head is very similar to that in *A. n. simonsi*, while the color of the back, wings, and tail is nearly identical with that of *A. n. seebohmi*. Ventrally it most nearly resembles *A. n. simonsi*, which has a less distinct breast band than does *A. n. seebohmi*, but it differs from both taxa in having almost no trace of a buffy wash on the abdomen and crissum. The mystacial streaks are dark gray and are less prominent than in either *simonsi* or *seebohmi*.

I have not examined specimens of *A. r. forbesi*, the isolated southern form, but

from the original description (Morrison, 1947) and the comments of Bond (1951) it is evident that its most noteworthy character is the presence of black on the forehead and in the circumocular area, which must make this race fairly similar to the northern forms of *A. nationi*.

Atlapetes albiceps

Range. The species is known from the western slopes of the Andes of southern Ecuador and northern Peru. There are records (Chapman, 1926, and specimens in MCZ and Basel Museum) from Paletillas, the Casanga Valley, and El Empalme in the southeastern part of the province of Loja, Ecuador, and a number of specimens have been collected in the Cerros de la Brea of adjacent Piura, Peru (Mus. Zool. Louisiana State Univ.; Basel Museum). Between here and eastern Lambayeque and western Cajamarca, from where there are several records, is a distance of about 200 km. The species is unknown between; presumably this gap will be filled when the area is better studied.

The vertical range is not readily determined because there are so few records with accurate altitudinal data. The species seems to occur from about 250 to 1,500 m. I have observed it at about 1,000 m in the Casanga Valley of Loja and ten specimens

from the Cerros de la Brea, Piura, were taken between 550 and 800 m.

Habitat. We found the species at Yamana, near the upper end of the fairly arid subtropical Casanga Valley. My limited experience seems to indicate that the bird is not uniformly distributed in the valley but occurs only where there are patches of denser scrub. This observation recalls similar comments made by Zimmer (1930) regarding *A. rufigenis*. In the heavily cultivated and grazed Casanga Valley these scattered patches are confined to the edges of the valley in the vicinity of brooks descending from the mountains, where the terrain is too steep to be used for agricultural purposes. It seems likely that the species once was more widely distributed.

Habits. Five specimens were taken in mid-October at Yamana. They seem to have constituted a single flock. All were in fresh plumage and with small gonads. Norton obtained two birds at Yamana in early July. These specimens were in very worn plumage and they too had small gonads. A female collected forty years ago on 17 May "on the Porculla road," Lambayeque (specimen MCZ), is quite worn, particularly on the tail; it is noted on the label that the ovary was slightly enlarged. From these bits of evidence it may be assumed that breeding probably occurs around January or February when the rainy season is at its peak.

The birds at Yamana were very shy. Their thin, high-pitched "seep" was usually the first indication of the presence of the species in the undergrowth. They were extremely active and called often as they moved through the underbrush and vines. They were seen most often in close vicinity of a stream. Apparently they obtained water or grit in the mud along the banks, for several birds had muddy bills and feet when collected.

Food. The stomach contents of five specimens taken in October were examined. All contained whole small seeds

and crushed larger seeds. Small quantities of ground-up insect material was found in four specimens. Only the leg of a hymenopteron, probably an ant, was identifiable. Considerable amounts of fine, sharp grit, predominately white or light colored, was present in all five specimens.

Morphological variation. *A. albiceps* differs from the four preceding species in having an extensively white forehead and (with the exception of the races *A. nationi nationi* and *A. n. brunneiceps*) in having a black rather than chestnut crown (Fig. 8). The white alar speculum immediately reminds one of *A. leucopterus*, or possibly of *A. s. schistaceus*.

There is a great deal of variation in the plumage of the head and throat of a series of six skins from Yamana and one from Lambayeque. The throats of two badly worn and heavily molting July specimens from Yamana are pure white but in the remaining five birds there are traces of mystacial streaks. These range from a single black feather to fairly pronounced, but unsymmetrical, streaks. In addition, one specimen has two dark feathers in the center of the throat.

The crowns of most specimens have scattered white filoplumes, particularly on the neck. A few white feathers at the edges of the black crown make for ragged borders on all specimens. One bird has a white feather in the center of the otherwise black nape and in the middle of the upper back. A single October specimen, presumably a young bird, is conspicuously brownish on the nape and reminiscent of *A. n. nationi*.

Birds in fresh plumage have a very thin white edge on the exposed base of the outer primary. The back is dark gray with a tawny wash, very similar to that of *A. nationi seebohmi*. The color of the venter is also extremely similar to that of *A. n. seebohmi*.

Measurements (Table 5) indicate that there is moderate sexual dimorphism in size (males larger) and that the tail is some-

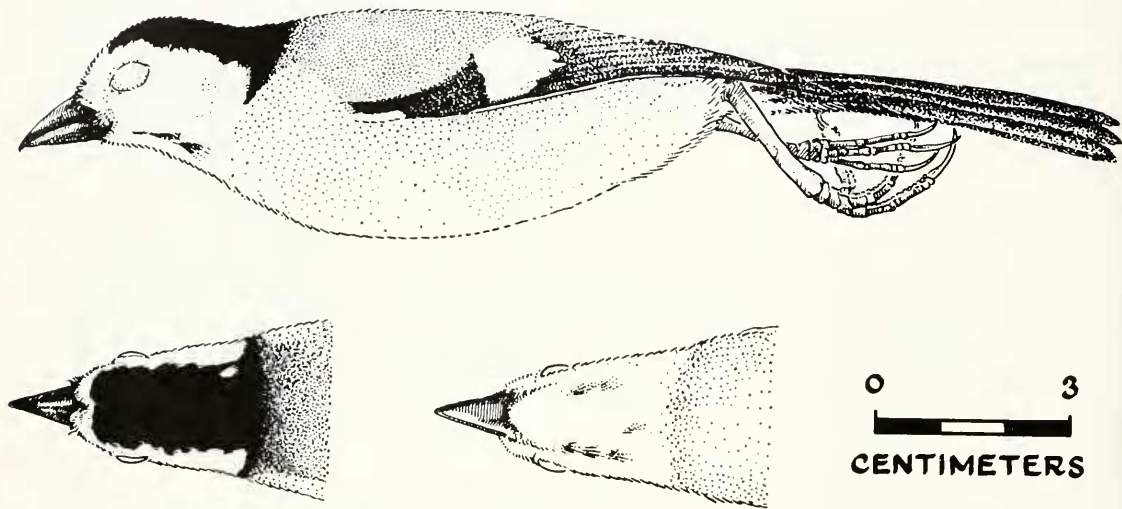


FIGURE 8. *Atlapetes albiceps*. Yamana (1,100 m), Casanga Valley, Loja, Ecuador. ♂. MCZ 288,116.

what shorter than the wing. These two characters are similar to the situation in *A. leucopterus*.

Atlapetes pallidiceps

Range. *Atlapetes pallidiceps* was described in 1900 by Sharpe from three specimens secured in May 1899 by the mammalogist P. O. Simons near Oña (1,900 m), Azuay, on the west side of the Andes of southern Ecuador. Hellmayr (1938), after examining the type series, reported that they had come from "Guishapa, Oña." Inquiries in the town of Oña in 1965 revealed no one with any knowledge of a locality by this name. Presumably "Guishapa" was an hacienda, now gone, or

possibly the name was incorrectly transliterated from the Quechua, the suffix *shapa* or *chapa*, meaning "sentry," being common in placenames in the region.

In the 65 years following the discovery of the species additional specimens were taken at Girón (2,100 m) and in the Yungilla Valley (ca. 1,500 m), both in Azuay and within 35 km of Oña. However, in all, not more than 10 specimens were known to be in museums prior to 1965 (personal observation).

In early November 1965 we went to Oña in the hope of observing the species. The region is extremely arid with very little naturally occurring vegetation, and even this is extensively cut for firewood and primitive cultivation. After considerable searching for a locality that would appear to be a likely habitat for an *Atlapetes*, we found an isolated pocket, about 10 km northwest of Oña, with a few hectares of artificially irrigated fields interlaced with shrubs and low trees bordering a brook that feeds into the Río Leon, which is about one kilometer to the east and several hundred meters lower. Here we discovered the species to be fairly common, although difficult to observe.

TABLE 5. MEASUREMENTS OF *A. ALBICEPS*.

		N	Range	Mean	SD
Wing	♂	2	80-82	81.0	2.31
	♀	3	77-81	78.3	
Tail	♂	2	73-77	75.0	1.16
	♀	3	70-72	71.3	
Culmen (fr. base)	♂	3	17-18	17.3	.58
	♀	5	16-17	16.4	.55
Weight	♂	3	36.6-39.0	37.5	1.28
	♀	3	34.9-36.1	35.6	.64

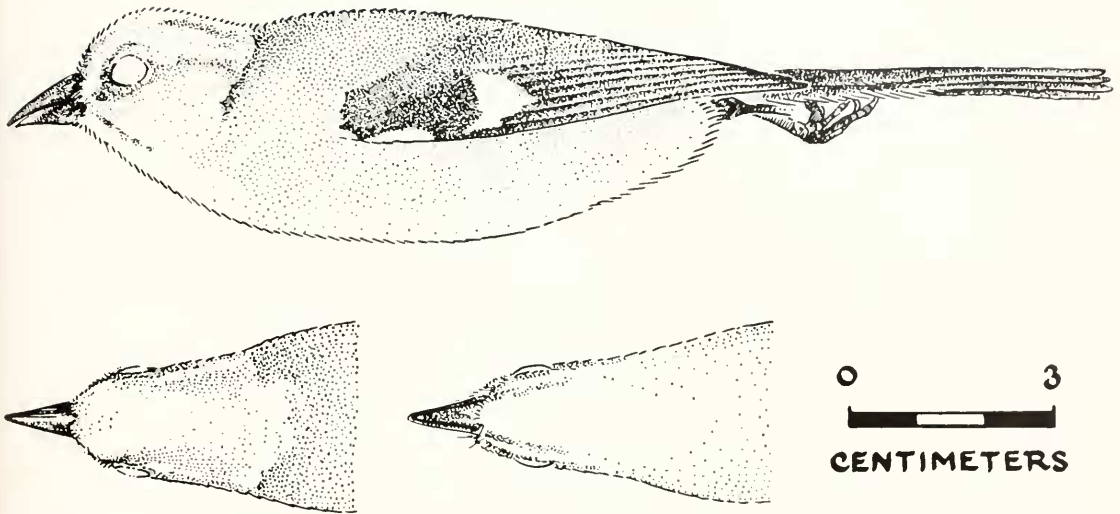


FIGURE 9. *Atlapetes pallidiceps*. 10 km north Oña (1,900 m), Azuay, Ecuador. ♀. MCZ 288,126.

The species is now known with certainty from three localities within an area no more than 35 km in diameter. It doubtless will be discovered beyond this restricted area, but I believe that it is almost a certainty that it is endemic to the valley of the upper Río Jubones and its tributaries. The presently known localities are on the Girón, Yungilla, and Leon rivers, all of which flow into the Jubones.

Habitat. We found the species in a small area of vegetation which stands as an oasis within the arid countryside. There was little thick undergrowth present, and the species occurred mainly in tree-sized acacias. It is not known whether the species normally frequents trees or is forced into them because of the absence of thickets.

Habits. Unlike other species of *Atlapetes*, we found *A. pallidiceps* to be arboreal to a great extent and, although shy, fairly conspicuous as it flew from tree to tree with its light-colored head appearing white against the foliage and sky. During our two days near Oña, a dozen specimens were obtained and others were sighted at least an equal number of times but were not collected. However, the species was

seen only once in a flock as large as three birds; the balance of the observations were of single individuals, or less frequently, of pairs.

The call, a thin "seep," which was heard on several occasions, seemed unusually weak for a bird of this size and less metallic than in other *Atlapetes* with which I am familiar.

A single bird was glimpsed on the ground in an area in which scraggly coffee was grown under taller shade trees. The bird appeared to be turning dead leaves by means of its bill rather than its feet. I have noted this use of the bill in several other *Atlapetes* species; it is believed by Skutch (1954) to be characteristic of the genus.

Food. The stomachs of eight birds were examined. All contained a good deal of sand, which at times made up almost half of the material in a full stomach. The food material in nearly all cases was ground to an unrecognizable state. Insect remains were found in six stomachs, the relative quantity ranging from very little to roughly one-quarter of the recognizable material. Most birds had relatively large pieces of what appeared to be endosperm from a big

seed. The outer coating was never attached to this material, and it seems likely that the seed was cracked before ingestion and the endosperm extracted in chunks. A few very small seeds (2 mm or less) of several types were also noted. A minute cocoon (5 × 2 mm) and a tiny (8 × 3 mm) larval coat of something like a fly larva were found in one specimen.

Morphology. *A. pallidiceps* is the most distinctive form of the species-group (Fig. 9), with its grayish white head and grayish olive back. However, when examined more closely, it appears merely to be a large version of *A. leucopterus dresseri* (particularly the variants in which there is a considerable amount of white circumocularly) in which the chestnut of the pileum has become grayish white and the black of the sides of the head has turned to dirty gray.

There is considerable variation in the color and markings of the crown and sides of the head in the 11 skins available to me (9 from near Oña, 2 from Yungilla). The area immediately above the bill is just slightly washed with tawny in a few specimens, but in others it is conspicuously rusty, and in one the whole center of the crown is also washed with this color. The dark lines in the crown and behind the eye are generally well delineated and separated by a pale line above the eye, but in some specimens darker feathers obscure the pale line, and in two birds the entire side of the head is dark. The crown ranges from dirty white to very pale brownish gray. The two specimens without pale and dark stripes on the sides of the head have the brownish gray of the back extended to the base of the pileum, thus restricting the pale area of the crown. The color of the back and rump varies slightly within the entire series but not so conspicuously as in the case of the head pattern and color. The amount and intensity of the tawny wash of the underparts varies. In some the wash is quite conspicuous on the throat, while in others it is entirely absent. In general this color is most intense

TABLE 6. MEASUREMENTS OF *A. PALLIDICEPS*.

		N	Range	Mean	SD
Wing	♂	3	74-80	76.3	3.21
	♀	6	72-77	75.0	2.09
Tail	♂	3	70-81	75.3	5.01
	♀	6	74-81	75.8	2.64
Culmen (fr. base)	♂	3	17-18	17.3	.58
	♀	6	16-17	16.5	.55
Weight	♂	4	33.4-35.3	34.0	.86
	♀	6	28.7-32.8	31.2	1.53

in a band across the breast, while it is blended with gray on the flanks.

A pale edge at the base of the outermost primary can be detected in a few specimens, but this trait is even less visible than in *A. albiceps*.

Mystacial streaks are evident in ten of the eleven skins examined. These are thin, faint, continuous lines restricted to the upper throat. They are not so conspicuous or so fragmented as in *A. albiceps*.

No sexual dimorphism is apparent in color, pattern, or linear measurements; the males may be slightly heavier (Table 6).

ORIGIN OF THE TAXA

In recent studies Haffer (e. g., 1967a, 1967b, 1969, 1970) has developed the convincing theory that the initial avifauna of the subtropical and humid temperate zones of the Andes was derived from that of the surrounding lowlands during the emergence of the Andes between the end of the Tertiary and beginning of the Pleistocene. And, further, that the multiplicity of present-day Andean taxa is the result of Pleistocene and post-Pleistocene climatic changes (cold-humid; warm-dry) and the associated changes in vegetation as well as altitudinal shifts in life zones, rather than because of orographic conditions. Although the geology and climatology of South America in the Pleistocene are known in no detail, thus making it impossible to determine with any precision the sequence and timing of the origins of the various taxa, the following appears to

be a plausible reconstruction of the history of the *A. schistaceus* species-group based on Haffer's theory.

The genus *Atlapetes* ranges in the mountains from Mexico to Argentina, with the overwhelming majority of species present in the northern Andes. Most of these occur in the subtropical or humid temperate zones, generally in forests or on their edges. It is a reasonable assumption that the present center of abundance of the component species coincides with the area in which the genus arose, but this is of no importance in the discussion that follows. However, granting this as well as accepting Haffer's thesis, it also seems reasonable to postulate that the genus developed in the subtropical or the humid temperate zone and that the *A. schistaceus* species-group had its origin in the subtropical zone, the zone in which it most frequently occurs today.

The stock from which the *A. schistaceus* species complex arose probably ranged from the northernmost Andes south to the present limit of the group's distribution, or possibly as far south as Bolivia and northern Chile. This was probably during one or more glacial cool-moist periods when the subtropical zone occurred at altitudes from about 500 m up to roughly 1,200 m and the treeless páramo zone began at 2,000 m or even somewhat lower (Haffer, 1970). At this time the subtropical forests must have existed in an almost continuous belt around the three Andean ranges in the north, and on the east and west sides of the Andes farther south. The total area covered by the subtropical zone probably was vastly greater than that occupied today, even though its vertical range was more restricted.

With the advent of an interglacial warm-dry period, of which there were several, doubtless of varying degrees of intensity, the subtropical zone retreated from the foothills and eventually may have been restricted to elevations between roughly 1,500 and 2,800 m (Haffer, 1970). The

subtropical zone existed, therefore, only on the higher mountains and thus was fragmented. In the region of southern Ecuador and northern Peru, where the Andes are on the average lower than elsewhere along the range and where deep valleys penetrate the mountains from both sides, the subtropical zone must have been particularly limited in area and much divided.

In conjunction with the upward movements in the life zones, owing to the warmer climate, there was also a radical change in precipitation and the type of vegetation it supported. According to Haffer (1967a; 1969), tropical forest largely disappeared from the Amazon basin and the northeastern lowlands and was confined to refuges, generally along the Andes. Presumably the lessened rainfall also affected the montane vegetation. Some areas that were high enough to support subtropical vegetation doubtless were covered by a nonforest type of growth. This would have been particularly true in the low area of southern Ecuador and northern Peru, a region of little rainfall even now. Here subtropical forest may have been entirely lacking, thus making a substantial breach in the distribution of any species dependent on this type of habitat.

Other major arid areas contributing to the fragmentation, restriction in range, and isolation of the avifauna of the subtropical forest were the upper valleys of the Cauca, Magdalena, Marañón, and Apurímac rivers. What occurred to the climate along the now arid coast of Peru and southern Ecuador during the warm-dry interglacials is unknown. Presumably the Humboldt Current existed then and affected the coastal and montane precipitation as it does now. If this is correct, it is probable that the treeless, and in places vegetationless, arid tropical zone extended higher on the western slopes of the Andes. The subtropical zone would, of course, have been correspondingly higher. It would also have been more restricted in extent than now because of the steepness of the mountains.

However, because the western slopes of the Andes of southern Ecuador and northern Peru derive their precipitation from winds coming off the Pacific, it seems likely that the subtropical zone here would have been less dry than, for example, the subtropical zone on the eastern slopes, which were above the dry, nonforested, areas of the Amazon basin. Pockets of fairly moist forest may have occurred on the western slopes wherever the Andes were high enough to deflect the moisture-laden westerly winds. Admittedly this is unproven and highly speculative, but the existence of such isolated pockets is strongly suggested when trying to account for the origin of certain species within the *A. schistaceus* complex.

A. schistaceus, a subtropical forest form that has a wider dispersal as well as greater vertical range than the five other species, exhibits a fragmented distribution (Fig. 1) that is explicable in light of the foregoing speculations. One of the most striking features of its present-day distribution is how closely this corresponds with the presumed locations along the Andes of interglacial forest refuges mapped by Haffer (1969, fig. 5).

In northeastern Colombia and adjacent Venezuela there is a group of subspecies (*fumidus*, *tamae*, and *castaneifrons*). Although the group is morphologically fairly distinct from other populations of *A. schistaceus*, the three races are weakly differentiated among themselves and probably were only recently and incompletely isolated from one another (see p. 299). The "Catatumbo" refuge occurred in this region.

The comparatively well-marked morphological differences between the group of three northern races and nominate *schistaceus* suggest that the distributional gap in the Eastern Andes of Colombia is real and relatively old. Similar gaps in this region are known for several species as, for example, the "coerebids" *Diglossa lafresnayii* and *D. humeralis* (Vuilleumier, 1969). The

arid Chicamocha Valley cuts deeply into the eastern Andes (Haffer, 1967b) and possibly acts as a barrier to species of the humid forest today and probably did so in the interglacials. As now known, nominate *schistaceus* seems to have isolated populations at the northern ends of the western and central Andes (Fig. 1). The two western isolates correspond to the "Nechi" refuge and the eastern isolate to an unnamed and generalized refuge along both sides of the eastern cordillera. The three isolates do not appear to be morphologically separable from one another or from the main population of *A. s. schistaceus*, which suggests that isolation is incomplete or recent.

It will be noticed (Fig. 1) that nominate *schistaceus* ranges well south on the slopes of eastern Ecuador but only for a short distance on the western slopes. These distributional patterns closely approximate the boundaries of Haffer's (1969) "Choco" and "Napo" refuges, respectively.

The species next appears in Peru on the eastern slope, roughly between the upper Marañón and the Ucayali (the race *taczanowskii*), and then reappears south of the Apurímac (the race *canigenis*). Both of these areas are depicted by Haffer as interglacial forest refuges.

The absence of *A. schistaceus* from the subtropical slopes of southwestern Ecuador, from along the entire western side of the Peruvian Andes, from the mountains of southern Ecuador and northern Peru, and from large segments of eastern Peru, is a second very striking feature in the distribution of the species. It will be noted that these areas are those in which no forest refuges were present during interglacial periods (see Haffer, 1969, fig. 5). Furthermore, the western Andean slopes presently unoccupied by *A. schistaceus* are adjacent to the arid coastal strip that seems likely to have extended onto and well up the slopes during the interglacial periods; the distributional breach in the mountains of southern Ecuador and northern Peru is the

area where subtropical forest was seemingly much restricted or absent at the same time; the distributional gaps in eastern Peru are in the vicinity of the arid valleys of the upper Marañón and Apurímac.

The presence of *A. schistaceus* where there were interglacial forest refuges, and the absence of the species where there were none, is certainly not coincidental. The only conclusion to be drawn is that the species was restricted to the refuges during one or more interglacial periods and that it has not been able to occupy subtropical forest that has developed since that time, either because of insufficient time or because of the presence of competitive species. The latter explanation seems to fit the evidence.

A. leucopterus and *A. nationi*, which occupy the western slopes from which *A. schistaceus* is absent, appear to be its counterparts to the north and south, respectively. Both species occur in habitats ranging from fairly arid scrub to moderately moist forest. This is a greater diversity than seems to be tolerated by *A. schistaceus* and may be because of their more varied evolutionary histories.

It appears that *A. leucopterus* arose as an isolate in western Ecuador during a warm-dry interglacial. It probably was derived from a population that was left behind in a less dry pocket on the slopes of the high mountains when, in the face of increasing aridity, *A. schistaceus* retreated to the moist Choco refuge. *A. leucopterus* would, then, have differentiated in a dryer habitat than that occupied by *A. schistaceus*. Later, as the climate became cooler but wetter, *A. leucopterus* was able to increase its range along with the expanding, but still relatively dry, subtropical forest. Later in the cycle it was able to accommodate to the change toward a more moist forest, a versatility still exhibited by the species. On the other hand, *A. schistaceus*, having arisen in moist forest and having taken refuge in moist forest

during the interglacials, was unable to exploit a drier habitat, thus permitting *A. leucopterus* to move into the newly available habitat and to expand its range until it abutted the range of *A. schistaceus* in northern Ecuador. The fact that they are not known to be sympatric is doubtless evidence of the close relationship and similar habits of the two species.

A. leucopterus dresseri, the race of southern Ecuador and northern Peru, appears to be a recent derivative of the nominate form. It is phenotypically highly variable, which argues against this assumption because peripheral, newly formed, populations are genetically less variable than the parent population. However, *A. l. dresseri* may be the product of various colonizations of scattered subtropical forests that occurred during interglacials in the southern Ecuador-northern Peru area and that are now merging into a single population but have not yet achieved morphological uniformity.

A. pallidiceps, the species which while large and distinctive is essentially not very different from *A. leucopterus* (see p. 314), seems also to be a derivative of nominate *A. leucopterus*. Its occurrence in an isolated small valley doubtless prevented it from being absorbed into the population now constituting *A. l. dresseri*.

A. nationi, the species of the western slopes of the Peruvian Andes, probably originated in a manner similar to that of *A. leucopterus*. A likely site would be some place within the area of northern Peru now occupied by *A. n. seebohmi*. *A. n. simonsi*, and *A. n. celicae* if it is a valid subspecies, are only slightly differentiated from *A. n. seebohmi* and probably are recent derivatives of that form. Because these races are restricted to somewhat higher altitudes and are less adaptable to a variety of habitats than is *A. l. dresseri*, they may be more recent arrivals. The partial sympatry of *A. albiceps* (see below) further suggests this to be the case.

A. n. nationi and *A. n. brunneiceps*, two

similar races that are abruptly and well differentiated from the three northern races of the species, seem to have been separated from the parent stock earlier. On the other hand, their distinctive characters (dark heads, brownish backs) could be the result of recent and minor genetic differences. *A. albiceps* may cast a light on this problem.

Immature *A. albiceps* is quite similar to nominate *A. nationi* and *A. n. brunneiceps*. The most conspicuous difference is that *A. albiceps* has a white alar speculum, a character entirely lacking in the species *nationi* and that immediately suggests affinity with *A. leucopterus*. Although conspicuous, the presence or absence of a wing patch is undoubtedly the result of a very small genetic difference. For example, nominate *A. schistaceus* has such a patch but its races do not. A similar situation is found in *A. rufinucha*. The race *latinuchus* has a speculum, whereas the other races lack it. Such a character can be of no value in determining specific affinities.

The presence of scattered white feathers on the heads of *A. n. nationi* and *A. n. brunneiceps* further suggests a tendency toward *A. albiceps*. It seems to me that *A. albiceps* was the earliest offshoot of *A. nationi* and that the dark-crowned races of *A. nationi*, with their scattered white feathers, are examples of an early stage of differentiation. In other words, in the process of differentiating, *A. albiceps* probably passed through a stage resembling that of *A. n. nationi* and *A. n. brunneiceps* and, given time, these two races may come to resemble *A. albiceps*.

The fact that *A. albiceps* regularly occupies a drier habitat than any other taxon within the group, with the exception of *A. pallidiceps*, may indicate that it entered northern Peru and southern Ecuador early, when the area was first recovering from a dry period. By having arrived early and having become well differentiated, the path was set for a second invasion of the parental form, *A. nationi*.

Only *A. rufigenis* remains to be considered. On geographical evidence alone one would postulate its derivation from *A. schistaceus*. The species is big and distinctive, but again the magnitude of the morphological differences probably does not reflect large genetic differences. As we have seen in *A. n. nationi* and *A. n. brunneiceps*, the loss of head pattern occurs readily. Size is an even more plastic character. Nominate *A. rufigenis* appears to have resulted from the isolation of a population of *A. schistaceus*, or its forerunner, in the arid upper Marañón valley. This could have occurred during a cold-dry interlude when *A. schistaceus* was retreating to the forest refuges on the Amazon slope. The valley is considerably lower than the surrounding mountains and could have served as a refugium. While there was little precipitation, the river may have supported ample vegetation for the continued existence of the bird. This would have been similar to the restricted habitat of *A. pallidiceps* nowadays.

It is less easy to account for the existence of the small isolated population *A. r. forbesi*, which is phenotypically quite similar to nominate *A. rufigenis*. I am, however, unable to picture a situation that would have allowed either taxon to have been derived from the other and that would not have involved resorption into *A. schistaceus*. I believe, instead, that this may be a situation where two peripheral isolates have responded morphologically to their isolation in a similar manner.

Perhaps one of the most interesting points revealed by this study is that while Haffer developed his theory of forested refugia to account for the origin of the varied avifauna of the tropical zone of the lower Andean slopes and adjacent lowlands, these refugia must have extended high in the Andes, at least to the subtropical zone, where they had an important role in differentiating various taxa within the *Atlapetes schistaceus* group (and doubtless among many species and genera

yet to be studied). However, in addition to the large refugia extending from the tropical lowlands well up into the Andes, smaller refugia must have occurred in moist pockets at high altitudes, and it is these localized refugia that led to the differentiation of the less widely distributed taxa, such as *A. pallidiceps*, *A. leucopterus*, and *A. nationi*.

SUMMARY

Atlapetes schistaceus, *nationi*, *leucopterus*, *rufigenis*, *albiceps*, and *pallidiceps*, from the northern Andes, are believed to have arisen from a common ancestor during the Pleistocene. They form the *A. schistaceus* species-group.

A. schistaceus, the most widely distributed of the six species, has a disjunct distribution from Venezuela to eastern Ecuador and eastern Peru. It occurs in the subtropical and temperate zones at altitudes from 1,850 to 2,500 m. Six races are recognized. The present distribution closely approximates the assumed locations of interglacial forest refugia. The species apparently arose during a cool-wet glacial period and was restricted, one or more times, to the forest refugia during warm-dry intervals. It seems unable to expand into more recently available suitable habitats because of competition from related species.

A. nationi ranges on the western slopes from southern Ecuador to southern Peru, in the temperate and arid subtropical zones, at altitudes from 1,870 to 3,500 m. There are five races. The species appears to be the southwestern counterpart of *A. schistaceus*. It probably was derived from a population of ancestral *schistaceus* that was isolated in a moist pocket in northern Peru during a warm-dry period.

A. leucopterus occurs only on the western slopes from northern Ecuador to northern Peru in both the humid and arid subtropics and in the arid temperate zone, from 600 to 2,900 m. There are two well-differentiated races. The taxon seems to be

the northern and central counterpart of *A. schistaceus* on the western slopes. Probably it was derived from an ancestral population left in a refuge in west-central Ecuador in a dry interval. The southern race is phenotypically highly variable and probably is a recent amalgam of isolated populations.

A. rufigenis is restricted to the eastern slope of Peru, in the drainage system of the Río Marañón and valley of Río Pampas. It occurs in the arid subtropical and humid temperate zone (a race in each) between 2,750 and 4,000 m. The species probably was formed from populations of *A. schistaceus*, or its forerunner, isolated in moist valleys during an interglacial period.

Monotypic *A. albiceps* occurs on the lower western slopes of southern Ecuador and northern Peru at altitudes between 250 to 1,500 m in the moderately arid subtropical zone. It is partially sympatric with *A. leucopterus* and *A. nationi*. It is fairly distinctive and is believed to have been an early derivative from *A. nationi*.

Monotypic *A. pallidiceps* is endemic to the arid valley of the upper Río Jubones of southeastern Ecuador, at altitudes from 1,500 to 2,100 m. Although superficially the most distinctive taxon of the species-group, it is believed to have been derived from nominate *A. leucopterus*.

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